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Hibernal Diapause of North American Papilionoidea and Hesperioidea

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Abstract. Information from 695 sources (mainly scientific journals) is presented on the life history stage in which 348 species of butterflies and skippers spend the winter in North America. *Parnassius, Neophasia,* many Theclini (especially *Satyrium*), most *Lycaena*, and a few others diapause as eggs. Coliadinae, Satyrinae, most Nymphalidae, Riodininae, two *Lycaena* of Palearctic affinity, many Plebejini, and most Hesperiidae diapause as larvae. Most Papilionidae, Pierinae, many Theclini (especially *Callophrys*), many Polyommatini, and a few others diapause as pupae. *Danaus plexippus, Anaea andria, Nymphalis, Polygonia,* and some *Vanessa* diapause as adults. Records from Japan and Britain are very similar. The boreal or arctic-alpine species which have a two-year life cycle generally pass the first winter as a young larva, the second winter as a mature larva. The life history stage in which winter is passed significantly influences the time of flight of adult broods during the year.

Introduction

Insects in temperate climates must survive the cold temperatures of winter. To do this, insects have a phenomenon called hibernal diapause. Diapause is an arrested state of development. Growth and feeding of larvae stop, embryonic and pupal development cease, and mating and reproduction (egg development) of adults do not occur. Diapause is usually noticed when rearing is attempted; when the immatures reach a certain stage, they do not feed or develop further, and unless special precautions are taken, they will desiccate and die. The basic function of diapause is to allow insects to endure an unfavorable time such as a freezing winter. The tropical species which stray into temperate climates usually do not have diapause stages, and they soon die in temperate zone winters. The native temperate zone species, however, spend the winter in a diapause stage. Insects in general can spend the winter in any stage, including egg, larva, pupa, or adult, but a given species is usually adapted to diapause in only one stage. A few species may be able to winter in several stages, however. Some alpine and arctic species which have a two-year life cycle may winter in different stages during the two winters, as noted below. Good general discussions of diapause are by Chapman (2), Danilevskii (4), Beck (1), and Lees (14).

Physiological and sometimes morphological changes occur during diapause. Growth stops during diapause. During winter diapause insects increase the concentration of glycerol, sorbitol, or alcohol in their bodies, which acts as antifreeze to lower the temperature at which they freeze. Free water is converted to a colloid-bound state, preventing damage from freezing (4). Insects in diapause respire at a rate much less than normal (454), and they are quiescent and do not feed or grow. Diapausing larvae usually have one extra instar, which is usually specialized for winter survival (132, 459). The hibernating generation of *Asterocampa* has six instars, versus 5 for the summer generation, for example. *Chlosyne gorgone* and *nycteis* have a special diapause instar with russet colored larvae (529, 97). *Plebejus icarioides* larvae turn brown in the second instar when they diapause, and are green before and after that (535, 536). *Euphydryas editha* has a special diapause instar with a thicker integument (548).

Diapause of adult butterflies such as *Nymphalis* takes the form of an arrested state of development of their reproductive system; the abdominal fat in females is not converted to eggs until diapause is broken.

Two environmental factors, sunlight and temperature, regulate the appearance of diapause in most insects (1, 2, 4, 14). The number of hours of sunlight during the day (the photoperiod) has been found to be the critical factor in starting diapause in most insects. Diapause occurs only when photoperiod is below a critical amount. One stage in the life cycle is sensitive to photoperiod, which causes that stage or (usually) a later one to undergo diapause. Egg diapause is usually initiated by short photoperiod experienced by females laying the eggs, larval diapause by short photoperiod experienced by an earlier larval stage, pupal diapause by short photoperiod experienced by the larva, and adult diapause by short photoperiod experienced in larvae or (in ladybird beetles) the adult. For example, *Limenitis archippus* diapauses as larvae (306), *Papilio polyxenes* as pupae (305), and *Pieris napi* as pupae (377). In all three species, the long days of spring and early summer prevent diapause, but the short days of late summer and fall act on the larva to trigger diapause. In some insects high temperatures prevent the onset of diapause and low temperatures may bring on diapause. High temperatures prevent diapause in *Lycaena phlaeas* (334). In *Pieris rapae*, diapause never occurs at 24 degrees C, but at 20 degrees C, the photoperiod experienced by the fourth-instar larva influences the pupal diapause; with 10-hour days all the pupae diapause, but with 13-hour days none diapause (289).

In many species including *Limenitis archippus, Pieris rapae* and *P. napi* the photoperiod mechanism differs between geographic locations (306c, 1, 14); the critical photoperiod allowing continued development increases with latitude, because the diapause mechanism has adapted to the local sunlight conditions at each latitude.

Many species with only one brood per year have obligatory diapause; when a particular stage is reached, diapause occurs regardless of normal environmental conditions. Examples are *Papilio indra fordi, Anthocharis cethura* (535), *Euphydryas phaeton* (393a), and many *Satyrium*. Physiologically, this usually occurs because the critical photoperiod allowing development is greater than that found at the latitude of the habitat. Extreme laboratory conditions (constant light and warmth) sometimes can prevent diapause in these species (4). Ecologically, obligatory diapause is generally due to the absence of food plants or other necessities later in the season.

Generally, prolonged exposure to cold in the winter is necessary to "break" diapause and allow the insects to resume growing when the weather warms. Long days also break diapause in *P. polyxenes* (305). Diapause may terminate spontaneously merely due to the passage of time (40a).

The net effect of these mechanisms is that development usually starts when the weather warms in spring, and ceases when photoperiod triggers diapause (most multivoltine species), or when the diapause stage is reached (in the obligatory-diapause univoltine species).

This paper discusses only winter (hibernal) diapause, but summer (aestival) diapause sometimes occurs as well (328). The same cessation of development occurs in aestival diapause as in hibernal diapause, but it usually occurs during a time of year when droughts are frequent. Adult diapause is difficult to recognize; it is suspected when lifespan is unusually long and mating and reproduction do not occur, and dissections of females reveal fat body but no mature eggs. *Coenonympha tullia* adults (40) and *Euphydryas* larvae (509) may diapause in the summer in California which has a mediterranean climate. *Ochlodes sylvanoides* has a short mature larval diapause in early summer in California (535). *Agathymus* larvae may aestivate (12). *Speyeria* species have only one generation per year, but the flight period is very long (usually mid June to mid September), and diapause seems to occur during it. Edwards (5) and Scudder (21) found that *S. cybele, aphrodite,* and *idalia* females do not lay eggs until late August or September. Scudder found that *S. cybele* eggs do not become full size inside the female until mid August, and in Virginia adults are rarely seen in July (they are apparently diapausing). *Speyeria coronis* and *zerene* also have an adult diapause in summer (296a). The physiological factors producing aestival diapause are not as well known as those for hibernal diapause. In general long days and high temperatures cause aestival diapause. A geometrid moth *Abraxes miranda* has a short aestival diapause caused by long days and moderate temperatures (1). Low temperatures cannot play a large role in breaking aestival diapause, because summer is warm.

Results

This section presents the available data on hibernal diapause stage. The data are arranged in several tables. Table 1 contains the mostly temperate zone species which almost certainly have evolved a diapause stage. Table 2 contains the species which probably do not have a true diapause. These are semitropical species or species which may migrate into temperate regions each year. These species are often reported to spend the winter in several different stages; species without diapause continue to develop so that all stages can be present at a given time whenever the weather is mild enough not to kill them.

These data are based on 623 literature sources, on personal communications from 27 scientists, and on 46 of my own records. I searched all of the major entomology journals which have many papers on butterflies, and nearly all of the major works and papers on butterflies. Some references have undoubtedly been missed, but it is significant that the last several hundred references examined produced very few species-stage records not already found. Because slightly more than half of the approximately 700 species found in North America lack data on diapause stage, future contributions to the subject will come from rearing this unknown fraction and the species inadequately studied before now.

The data are cited by number (see Literature Cited). Authors of scientific names are not listed; they can be found in the references cited. The taxonomy of (427, 13, 12) is used except for recent changes that will appear in my forthcoming "Field Guide to North American Butterflies."

Discussion and Conclusions

Table 3 summarizes winter diapause information for nearctic species with adequate data, and compares it to Japanese (348) and British (11) information. Results are very similar among all three faunas. *Parnassius* usually diapause as eggs, but the remaining Papilionidae diapause as pupae. In the Pieridae, the Coliadinae usually diapause as larvae whereas the Pierinae usually diapause as pupae. Among the Nymphalidae, the Satyrinae and most other Nymphalidae almost always diapause as larvae, although *Anaea andria*, and the genera *Polygonia, Nymphalis, Aglais,* and some *Vanessa* (these four are closely related) diapause as adults. Among the Lycaenidae, the Theclini diapause as eggs usually, except for a large section (mainly *Callophrys*) that diapauses as pupae. Most American *Lycaena* diapause as eggs, but two American species (*phlaeas* and *cupreus*) belong to a Palaearctic group which diapauses as larvae. The Polyommatini usually diapause as larvae, occasionally as eggs or pupae. The Riodininae studied diapause as larvae. Hesperiidae usually diapause as larvae.

The larval diapause species are usually specialized to diapause as young, part-grown, or mature larvae. Most diapause as part-grown larvae, but a few (*Cercyonis, Speyeria,* and others) diapause as first instar larvae, and *Everes,* most Pyrginae, and several others diapause as mature larvae.

Several-year diapause of annual species. Occasionally species with life cycles of one year or less have longer life cycles because diapausing individuals do not emerge in spring but emerge only after another year or more in diapause. *Euphydryas chalcedona* larvae sometimes diapause for up to five years (54), and *E. editha* sometimes diapause for 2 years as larvae (138). Many pupal diapause species are known to do this (5, 385), including *Papilio aristodemus* (13, 377b), *P. cresphontes* (21, 95), *P. bairdii* (170), *P. zelicaon* (538, 315a, 335a), *P. polyxenes* (234, 101), *P. p. rudkini* (503, 477a, 22a, 427--six years), *P. indra* (412), *P. multicaudata* (167), *P. glaucus* (234), *P. g. rutulus* (167), *Eurytides marcellus* (234), *Anthocharis sara* (471, 167, 343a, 387a, 477a), *A. cethura* (471, 477a, 167, 535--five years), *A. lanceolata* (254, 477a, 421), *A. midea* (167, 234), *Euchloe ausonides* (167, 477a), *E. hyantis* (477a), *Pieris rapae* (482), and *Pieris sisymbri* (477a, 535--five years). Eggs might also diapause for several years. Several-year diapause would seem to be a useful adaptation to avoiding unfavorable years (290). Emergence of *Papilio aristodemus* (377b), *Anthocharis cethura* and *Euchloe hyantis* (535), seems to be stimulated by moisture in addition to cold. *Papilio polyxenes rudkini* and *Chlosyne neumoegeni* have summer and fall broods that seem to emerge from diapause as a response to rain; the more the rain, the larger the emergence (535).

Diapause stage of biennial species. Some boreal, arctic, and alpine species always have a two-year life cycle. They fly as adults only on alternate years, or at a given locality there are even-year and odd-year cohorts which rarely or never interbreed. Table 4 lists the species which are biennial, and summarizes the data on diapause stages from Table 1 for these species. For *Parnassius eversmanni* diapause occurs as an egg the first winter, then pupa the second winter, so that larval feeding occurs only on alternate years. For most other species, however, which include two *Colias, Chlosyne damoetas* (probably biennial), *Boloria alberta* ?, and seven *Oeneis,* the young larva spends the first winter, and the older or mature larva spends the next winter. This interpretation nicely explains the data on winter stages of *Oeneis,* which otherwise seem contradictory or confusing. Many other species of *Erebia, Boloria,* etc., are suspected of being biennial.

One very interesting aspect of biennialism is that when several biennial species occur together, they often fly on different years. For instance, *Oeneis chryxus* and *Neominois ridingsii* fly on Sonora Pass, Mono Co., California, at the same sites, *chryxus* in odd years, *ridingsii* in even years. *Oeneis jutta* and *O. chryxus* alternate years in Michigan, *O. jutta* and *O.* (*nevadensis*?) *macounii* alternate years in Minnesota. Adult interference during mate-locating behavior or larval competition may cause these species to fly in alternate years. Larval feeding in biennial species may be concentrated or restricted to alternate years. In eastern Alaska around Fairbanks, however, *O. jutta, O. polixenes, Erebia disa, Boloria astarte distincta, B. polaris, B.* (*titania*?) *chariclea*, and *Hesperia comma* all fly in odd-numbered years. In such cases perhaps the weather was so unfavorable in the past in an even-numbered year that all the adult cohort failed to mate and reproduce, and only the cohort occurring on the odd-years survived. Collectors returning from the far north often report such weather. Eventually, when more of the cohorts for biennial species have been discovered and mapped, a comparison with Pleistocene climatic events may help elucidate these patterns.

Non-diapause species. Contradictory information sometimes occurs for subtropical species which have no definite diapause stage (Table 2). Since these species develop during the winter, they may be found then in any stage. For instance, *Ascia monuste* develops year-around in Florida, and freezing winters kill the entire population (47). Some species such as *Euptoieta claudia* and *Precis coenia*, which have been reported to spend the winter in several stages, are warm-weather species which may actually have no diapause stage. Several species (*Colias eurytheme*, *Vanessa cardui*) may or may not have a true diapause. Hovanitz (525) and Shapiro (318) think that *eurytheme* may not have a true diapause, but the best data for this species indicate that it passes the cold winters in the larval stage as do its congeners with a true diapause. It has expanded its range northward within the last 100 years and may not have adapted yet to northern latitude photoperiods. Its close relative *C. philodice* has a similar pattern of winter stage records (Table 1). Williams (377a) states that *cardui* does not survive the U. S. winter in any stage, although many other authors (Table 1) give the adult as the most probable winter stage (as in other *Vanessa*), and Baker (304) thinks it may survive the British winter. *Danaus plexippus* diapauses as an adult, but mainly in Mexico and along the California coast (391, 426); it may not be able to tolerate temperatures far below freezing.

Ecological significance of hibernal diapause stage. The main benefit of a hibernal diapause stage is winter survival. Another significant feature is that the diapause stage is correlated with the seasonal appearance of the adults and other stages during the season. The adult diapause species fly first in spring, followed successively by pupal, mature larval, half-grown larval, young larval, and finally egg diapause species. The first instar diapause species often emerge as late in the season as the egg diapause species, because at least two of the egg diapause species (*H. comma, T. lineola*) actually diapause as first-instar larvae inside the egg. This seasonal progression is very striking among the univoltine species and among the first yearly brood of multivoltine species in Colorado (529, 536). It means that insect diapause strategies are adapted to the phenology of their host plants and habitats. The hibernal diapause stage may be adapted to the host plant in other ways. The egg diapause species commonly place their eggs on the larval host plant where the larvae will not need to search for food in spring. *Lycaena* usually diapause as eggs haphazardly placed around *Rumex* plants. The larval diapause species may or may not need to search for their host plants in spring, depending on where they diapause. The *Limenitis* (*Limenitis*) species diapause as larvae inside a cut-leaf case called a "hibernaculum," usually attached to the tree. *Speyeria* larvae sometimes diapause inside grass stems, and Melitaeini larvae commonly diapause under stones or logs. Many Pyrginae larvae diapause inside their silk tubes constructed from dicotyledon leaves, which fall to the ground in fall. The pupal and adult diapause species do need to search for the host plants in spring. The adult diapause species generally mate in early spring after spending the winter in crevices such as under bark (*Nymphalis, Polygonia*) or hanging from trees in dense aggregations (*D. plexippus*). It is conceivable that larval mortality may be high in spring for larvae which must relocate their host plants. The egg diapause species tend to have fewer broods than other species in Colorado; eggs may be better protected against desiccation than other diapause stages except pupae, so may be able to live longer.

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C. Personal records of J. Scott. Number 529. Most records are for Colorado; some are for California and elsewhere.

D. Records based on personal communication (numbers 530-554). 530 Richard A. Arnold, 531 Auburn E. Brower, 532 Lincoln P. Brower, 533 F. Martin Brown, 533a Robert P. Dana, 534 Scott L. Ellis, 535 John F. Emmel, 536 Marc Epstein, 537 Clifford D. Ferris, 538 Michael S. Fisher, 539 Jack L. Harry, 540 J. Richard Heitzman, 541 Roy O. Kendall, 542 Sterling O. Mattoon, 543 Lee D. Miller, 543a Douglas Mullins (pers. comm. to John F. Emmel), 544 Erval J. Newcomer, 545 Kilian Roever, 546 Arthur M. Shapiro, 547 Steven R. Sims, 548 Michael C. Singer, 549 Ray E. Stanford, 550 Fred T. Thorne, 551 David L. Wagner, 552 Ralph E. Wells, 553 Michael Young, 554 Steven Stone.

Table 1

Hibernal diapause stage for temperate zone species which probably have a true diapause. Diapause stage: E-egg, L-larva (instar given in arabic numbers, or y-young larva, h-part or about half grown larva, m-mature larva), P-pupa, A-adult. Diapause stage for biennial species is indicated by I-first winter, and II-second winter. e-probably an error; diapause probably occurs in the other stage listed for the species (some sources cited after an e may prove that diapause does not occur in this stage). r-winter rarely spent in this stage.

SPECIES	HIBERNAL DIAPAUSE STAGE	SOURCE
Papilionidae		
Parnassius phoebus	E-I	473, 449, 230, 5, 99, 131, 135, 536, 16, 529
	L (h, nearly m)-II	5, 536, 330a, 160a (L or P), 22a
Parnassius clodius	E-I	449, 99, 131, 135
	L (h or m)-II	535, 22a
Parnassius eversmanni	E-I	348
	P-II	348
Papilio glaucus	P	13, 9, 19, 20, 21, 540, 433, 5, 23, 58, 234, 431, 232, 234, 73, 62, 66
Papilio glaucus rutulus	P	532, 58, 546, 5, 15, 167
Papilio eurymedon	P	532
Papilio multicaudata	P	532, 272, 366, 5, 167, 251, 554
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Lethe anthedon	L(3-4)	13, 299, 20, 540, 21, 123, 5, 8, 15, 23, 423, 433, 19, 232
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Boloria eunomia	L(3)	12, 160, 529
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Hesperia miriamae	E?	521
Hesperia sassacus	P?	20, 21, 13, 433, 19
Hesperia viridis	L?	370
Euphyes bimacula	L(h)	529
	P?	19
Euphyes dion	L(3)	540
Euphyes vestris	L(3)	314, 540
Pompeius verna	L?	13, 219
	P?	219
Poanes zabulon	L(m)?	19, 20, 21
	P?	19, 20, 21
Poanes viator	L or P	373
Poanes hobomok	E, L, P?	437, 225, 15, 249, 218, 242, 433
Polites sabuleti	P	317
Polites mardon	P	317
Polites themistocles	P	225, 13, 511, 23, 19, 20, 21, 433, 218
	L?	218
Polites coras	L(1-5)	433, 506, 13, 299, 20, 21, 19
	P	506, 433, 13, 299, 20, 21, 19
Polites origines	L(3-4)	13, 510, 19, 218
	P?	19
Polites mystic	L(4)	226, 423, 507, 19, 21, 20, 13, 433
Ochlodes sylvanoides	L(1)	331, 427
	E?	427
Paratrytone melane	L?	486

Problema byssus	L(4)	371, 12, 540
Atrytone logan	L?	13, 423, 19
	P?	13, 423
Atrytone arogos	L(4 of 6)	327, 540, 481
Panoquina panoquinoides errans	L	485
Wallengrenia egeremet	L(h)	13, 423, 433, 19, 218, 249
Amblyscirtes hegon	L(1)	399
	P?	19
Amblyscirtes celia belli	L(4)	316
Amblyscirtes nysa	L(h-m)	315, 540
Amblyscirtes aenus	L(h)	529
A. aenus linda	L	540
Amblyscirtes vialis	L	540
	P(e)	19, 13, 423, 23
Atrytonopsis hianna	L(m)	329, 540
Megathymus yuccae	L(h-m)	12, 495, 39, 25, 326, 517, 25b, 25c
Megathymus ursus	L(3, 4, 5)	12, 25b
M. ursus violae	L(h)	529
Megathymus cofaqui	L	263
M. cofaqui harrisi	L	9
Megathymus streckeri texanus	L	271
Megathymus streckeri streckeri	L	26a
Stallingsia smithi maculosus	L	350
Agathymus neumoegeni	L(1-3)	311, 38
Agathymus polingi	L(1-3)	311
Agathymus evansi	L(1-3)	311
Agathymus aryxna	L(1-3)	311, 12
A. aryxna baueri	L(1-3)	311
A. aryxna freemani	L(1-3)	311
Agathymus alliae	L(1-3)	311, 12
Agathymus mariae	L	313, 224

Table 2

Species which probably have no diapause stage. These are mainly subtropical species or migrants to temperate areas. For explanation of symbols see Table 1. n- source states that no diapause occurs.

SPECIES	WINTER STAGE	SOURCE
Papilio palamedes	P	13, 23, 366(n), 19, 114
	L	13, 23
Nathalis iole	A	540, 296b(n)
	P	233
Phoebis sennae	A	15, 23, 21, 20, 19
	P?	232
	L?	21, 20, 19
Phoebis agarithe	L(y)	297
Eurema lisa	A	15(n), 23, 12, 13, 482(n), 20, 19(n)
	P	12, 13, 232
Colias cesonia	A	327(n), 273, 404, 277, 540
	P	13, 427, 232, 363a, 370a(n)
Ascia monuste	L, P, A	302, 47(n)
Euptychia hermes	L	320, 366(n), 13, 232
Agraulis vanillae	L, P, A	332a(n), 395(n), 288(n), 232, 364a, 260a(n), 370a(n)
Euptoieta claudia	A	23, 423, 540, 21, 13, 225, 12, 20, 19, 232, 277
	P	23, 540, 21, 20, 19
	L	23, 8, 21, 20, 19, 16, 277
Precis coenia	A	232, 482, 23, 13, 12, 540, 433, 327(n), 520(n), 19, 20, 21
	P?	546, 387
	L	546, 529, 387
Calephelis nemesis	L or P	487
Ministrymon leda	P?	501
Strymon columella	L?	498
Panoquina ocola	L or P	364
Nyctelius nyctelius	L	301
Lerodea eufala	L, P?	264
Polites vibex	L or P	370
Atalopedes campestris	A?	13
Lerema accius	P?	13, 19
Perichares philetes	L	301
Calpodes ethlius	L or P	370, 482(n), 260a(n)
Urbanus proteus	A	225, 19
Heliopetes macaira	?	370(n)
Heliopetes laviana	L	370
Phocides polybius	L	356
Cogia calchas	L	372

Timochares ruptifasciatus	L	389
Cabares potrillo	L	389
Xenophanes trixus	L	389
Chioides catillus	L	372, 370
Staphylus mazans	L or P	370
Chiomara asychis	?	389(n)

Table 3

Hibernal diapause stage of Nearctic, Japanese, and British butterflies (E-egg, L-larva, P-pupa, A-adult).

	Nearctic				Japan				Britain			
	E	L	P	A	E	L	P	A	E	L	P	A
1. Papilionidae												
Parnassius	3	2	1		3		1					
other Papilionidae			17				13				1	
2. Pieridae												
Coliadinae		10		1		2	1	4		2	1	1
Pierinae	1		13			3	5				3	
3. Lycaenidae												
Theclini	17		21		25	1	2	3	4		1	
Miletini						1						
Curetini								1				
Lycaenini	12	2				1				2		
Polyommatini	1	10	10		4	8	4		2	9	1	
Riodininae		6									1	
4. Nymphalidae												
Polygonia, Nymphalis, Aglais, Vanessa				12				10				6
Anaea				1								
Danainae				1								
Satyrinae		27				18	1	1		10		
other Nymphalidae		52	1		2	23	3	1	1	8		
5. Hesperiidae	3	59	7		2	13	2		2	5	1	
Total	37	168	70	15	36	70	32	20	9	36	9	7

Table 4

Biennial species: hibernal diapause stage, cohort of adult flight (even or odd years), and documentation of biennialism. Diapause stages from Table 1.

SPECIES	HIBERNAL DIAPAUSE STAGE	ADULT FLIGHT TIME & LOCATION	DOCUMENTATION FOR BIENNIALISM
Parnassius eversmanni	E-I P-II	Japan	348
Parnassius phoebus, clodius	E-I, L-II	-----	-----
Colias meadii	L(1)-I L(3-4, 5 [r])-II	Alberta	162
Colias nastes	L(y,3,m)-(I+II?) P?	-----	-----
Colias hecla	L(I+II), P?	-----	12, 13
Chlosyne damoetas	L(y)-I? L(3-4, 5?)-II	every yr. Colo.	529
Boloria alberta	L(1)-I L(h or m) or P-II	mostly even yrs. Alberta, mostly odd yrs. Plateau Mtn. Alberta	5, 200, 247, 529, 398a 414b, 12
Boloria astarte	-----	even yrs. Washington, even and odd yrs. Alberta	414b, 12, 17, 529, 398a
B. astarte distincta	-----	mostly even yrs. in north, mostly odd yrs. in south	*, 370b
Boloria polaris	-----	odd yrs. central Alaska, Manitoba, mostly even yrs. rest of range	*, 385, 329a, 393d, 422c, 414c, 331a
B. (titania?) chariclea	L(1,4) (*titania*)	odd yrs. Alaska, Yukon	*, 370b
Oeneis jutta	L(1, 2, 3)-I L(4, 5, 6)-II	odd yrs. Alaska, Michigan, Wisconsin, Minnesota, Saskatchewan; even yrs. Colo., Manitoba, Newfoundland, Ontario, New Brunswick, Maine, Labrador, Quebec	385, 42, 168, 25a, 419a, 417a, 398b, 414c, 529, 10, *, 377c, 422c, 422a, 414a, 329a, 331a
Oeneis polixenes	L(1, perhaps 2-3)-I L(4, 5)-II	odd yrs. Alaska; even yrs. Maine	*, 351a, 422c

Oeneis melissa	L(y, 2, 3)-I L(5)-II	every yr. Colo.	167, 5, 19
Oeneis uhleri	L(2, 3, 4, 5)(I+ II?)	biennial Alberta; may be more common odd yrs. Colo.	5, 529
Oeneis nevadensis	L(2,3)-I L(5)-II	even yrs. Wash., Vancouver Island; mostly even yrs. Oregon & Sonoma Co. Calif.	395a, 5, 369, 17, 385, 398, 332, 422e, 12, 344a, 300
Oeneis (nevadensis?) macounii	L(1, 2)-I L(m)-II	odd yrs. Alberta, Saskatchewan, Riding Mts. Manitoba; even yrs. eastern Manitoba, Ontario, Minnesota	167, 385, 10, 374a, 422a, 398c, 168, 175, 375a
Oeneis chryxus	L(1, 2)-I L(3,4,5)-II	even yrs. Michigan & so. Colo., odd yrs. Sonora Pass Calif.; mostly odd rest of Calif. (*ivallda*)	385, 529, 307, 416, 422e
Oeneis taygete	-----	odd- & even-yr. cohorts differ in phenotype in N. Wyoming; even yrs. Labrador	385, 537, 414c, 543, 414
Oeneis alberta	-----	biennial Colorado?	553
Neominois ridingsii	L(2[r], 3-4)+?	even yrs. Sonora Pass Calif.	529
Erebia disa	-----	odd yrs. Alaska, Saskatchewan; even yrs. part of Saskatchewan	*, 385, 10, 318a, 422c
Erebia theano	L(y)+?-I&II	even yrs. throughout Colo.	385, 529
Hesperia comma	*E* + ?	odd yrs. Alaska; even yrs. Churchill Manitoba	*, 329a
Pyrgus centaureae	-----	mostly odd yrs. Colo.	529

*references 405, 406, 407, 408, 409